

A morphometric analysis of cranial variation in Holarctic weasels (*Mustela nivalis*)

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Abstract

Morphometric relationships of Holarctic weasels (*Mustela nivalis*), based on cranial variables, were analyzed by multiple discriminant function analysis. The results show that all geographic populations of this weasel, except the Egyptian weasel (*subpalmata*), form part of a morphological continuum, thus supporting the contention that they represent one species. The greatest amount of variation is found in the western Palearctic, which suggests that the species has a long history in that part of the world and probably evolved there. The morphometric groupings do not correspond to current infraspecific classification in detail. A division of *M. nivalis* into three subspecific groups is supported by the data. These are: 1. *nivalis*, comprising all small forms of the boreal zones of the Holarctic Region; 2. *vulgaris*, the intermediate to large forms inhabiting the temperate and mediterranean areas of the western Palearctic and 3. *pallida*, a central Asian form. The evidence suggests that the Egyptian weasel is a separate species, *M. subpalmata*.

Introduction

The least weasel (*Mustela nivalis*) has an extensive Holarctic distribution stretching from North Africa and Europe across Asia into North America. Over this vast area this mustelid displays such an unparalleled degree of variation, particularly in size, that the systematic relationships among different geographic populations have long been uncertain.

More than five decades ago, G. M. ALLEN (1933) combined the small forms from North America and northern Asia into one species. In this regard he followed KURODA (1921), who had previously described a new Japanese form as a subspecies of the North American least weasel (*M. rixosa*). Shortly after, OGNEV (1935) recognized a single species of small weasel, *M. nivalis*, in the Palearctic Region, a view shared by ELLERMAN and MORRISON-SCOTT (1951). The latter authors stated that the same species perhaps also occurred in North America. On that continent most mammalogists, following HALL (1951) and HALL and KELSON (1959), continued to regard the North American least weasel as a distinct species, *M. rixosa*. Later, HALL (1981) changed his opinion and included the American form in *M. nivalis*, citing REICHSTEIN (1957) for the change. However, REICHSTEIN's study focused on geographic variation and sexual dimorphism in Europe. The analysis of his data led him to the conclusion that the small morph ("Zwergwiesel", *M. minuta* Pomel) is not specifically distinct from the larger morph ("Mauswiesel", *M. nivalis* L.). However, the conclusion that North American and Eurasian small morph weasels are conspecific was not based on his own analysis, but REICHSTEIN (1957) attributes it to a personal communication from ZIMMERMANN. Subsequent studies on large numbers of skins and skulls from Europe (MAZAK 1970), on chromosomes (MANDAHL and FREDGA 1980) and experimental cross-breeding (FRANK 1985) all support the earlier conclusion that there is only one species *M. nivalis* in Eurasia and that the small form is only subspecifically distinct. Cytogenetic comparisons of Eurasian and North American weasels (JARRELL 1983) extend this support to the inclusion of the Nearctic least weasel, *M. rixosa*, in *M. nivalis*. Despite

the evidence in support of a single species, the belief that two species coexist in some areas continued to persist and some authors (KURTÉN and ANDERSON 1980; CORBET 1987) maintained that the taxonomic uncertainty had not been adequately resolved. The lack of direct morphometric comparisons among populations from the entire distributional range has, undoubtedly, contributed to the persistence of this uncertainty. The present study aims at filling this lacuna, by taking a global view of the morphometric interrelationships among populations across the entire Holarctic range.

The objectives of the present study are to: 1. analyze and describe cranial variability in *M. nivalis* across its entire distributional range, using a multivariate approach; and 2. reevaluate the taxonomic status and evolutionary relationships of small and large morphs.

Materials and methods

The total sample on which this study is based, comprised 542 adult skulls, including 263 skulls examined and measured by me, supplemented by data on 279 skulls published by REICHSTEIN (1957). The breakdown by subspecies, sex, locality and collection of the specimens examined, arranged by nominal subspecies and geographic subsamples, is as follows: BM = British Museum of Natural History; USNM = U. S. National Museum of Natural History; NMC = Canadian Museum of Nature; APM = Alberta Provincial Museum.

M. n. nivalis: 12 males, 2 females, 3 undetermined. Northern Europe: males, Norway 1 (BM); Sweden 1 (USNM); females, Russia 1 (BM); Western Siberia: males, 10 (NMC); females 1 (BM); undetermined 3 (BM).

M. n. vulgaris: 47 males, 15 females, 3 undetermined. Western Europe: British Isles, males 9 (BM), 5 (USNM), females 5 (USNM), undetermined 2 (USNM); France, males 6 (BM), 4 (USNM), females 1 (BM), undetermined 1 (BM), Netherlands, males 12 (BM), females 2 (BM), 1 (USNM); Central Europe: Czechoslovakia, males 1 (USNM), females 1 (BM), Hungary, males 1 (BM), Germany, males 3 (BM), females 1 (USNM), Roumania, males 1 (USNM), Switzerland, males 5 (USNM), females 4 (USNM).

M. n. boccamela: 30 males, 10 females, 3 undetermined. Italy and Mediterranean France: France, males 1 (BM); Italy, males 3 (BM), 4 (USNM), females 1 (BM), undetermined 1 (BM), Sardinia, males 2 (BM), Sicily, males 2 (BM), Balkan Peninsula: Greece, males 1 (BM), Crete, males 1 (BM), Yugoslavia, males 3 (BM), females 1 (BM), Iberian Peninsula: Spain, males 5 (BM), 1 (USNM), females 2 (BM), 2 (USNM), undetermined 1 (BM), Azores, undetermined 1 (BM), Balearic Islands, males 1 (BM), females 1 (BM); Southwestern Asia: Afghanistan, males 1 (BM), Turkey, males 4 (BM), 1 (USNM), females 1 (BM), 1 (USNM), Iran, males 1 (BM), females 1 (BM).

M. n. numidica: 3 males, 1 undetermined. Northwest Africa: Algeria, males 2 (BM), Morocco, males 1 (USNM), Tunis, undetermined 1 (BM).

M. n. subpalmata: 8 males, 9 females, 2 undetermined. Egypt: males 3 (BM), 5 (USNM), females 3 (BM), 6 (USNM), undetermined 2 (USNM).

M. n. pallida: 6 males, 1 undetermined. Central Asia: Djarkent (= Panfilov), males 6 (BM), undetermined 1 (BM).

M. n. pygmaeae: 24 males, 5 females, 1 undetermined. Eastern Siberia: males 21 (USNM), females 4 (USNM), Eastern Asia: Korea, males 1 (USNM), females 1 (USNM), Manchuria, males 2 (USNM), undetermined 1 (USNM).

M. n. russelliana: Szechwan, females 1 (BM).

M. n. rixosa: 26 males, 15 females, 2 undetermined. Canada: Alberta, males 2 (NMC), 6 (APM), females, 2 (NMC), 5 (APM), undetermined 1 (APM), British Columbia, males 5 (NMC), Manitoba, males 1 (NMC), Northwest Territories, males 3 (USNM), 4 (NMC), females 2 (NMC), undetermined 1 (NMC), Quebec, males 1 (NMC), Saskatchewan, males 4 (NMC), females 6 (NMC).

M. n. allegheniensis: 11 males, 4 females. Eastern United States: Indiana, males 5 (USNM), females 1 (USNM), Maryland, females 1 (USNM), North Carolina, males 1 (USNM), Pennsylvania, males 1 (USNM), females 1 (USNM), Tennessee, males 1 (USNM), Virginia, males 1 (USNM), West Virginia, males 2 (USNM), females 1 (USNM).

M. n. campestris: 7 males, 3 females; Central Great Plains: Missouri, males 2 (USNM), females 2 (USNM), North Dakota, males 3 (USNM), South Dakota, males 2 (USNM), females 1 (USNM).

M. n. eskimo: 4 males, 4 females, undetermined 2; Alaska-Yukon: Alaska, males 1 (USNM), 1 (NMC), females 3 (USNM), undetermined 1 (NMC), Yukon, males 2 (NMC), females 1 (NMC), undetermined 1 (NMC).

There is no generally accepted subspecific classification of *M. nivalis*. In the main, I have followed ELLERMAN and MORRISON-SCOTT (1951) in the application of subspecific names to Palearctic populations, with some modifications based on HEPTNER et al. (1974). For North American forms I have followed HALL (1981). Specimens of undetermined sex were diagnosed by discriminant function analysis and included in the appropriate sample.

Thirteen measurements were made on each skull, using a digital caliper capable of measuring to 0.01 mm. The cranial measurements taken (as defined by VAN ZYLL DE JONG 1972, except for #1), are: 1, condylobasal length (CBL); 2, interorbital width (IOW); 3, width between postorbital processes (WPOP); 4, orbitonasal length (ONL); 5, width of the postorbital constriction (WPOC); 6, basal skull width (BSW); 7, mastoid width (MW); 8, zygomatic width (ZW); 9, buccal length of P4 (LP4); 10, greatest width of P4 (GWP4); 11, lingual length of M1 (LM1); 12, greatest diameter of M1 (GDM1); 13, length of the mandibular premolar-molar series (Lpm). Measurements 1, 2, 7 and 8 were supplemented with data from REICHSTEIN (1957).

Multigroup discriminant function analysis (BIOSTAT II MDA, PIMENTEL and SMITH (1986) was used to discriminate among geographic samples of weasels using 12 variables. This analysis was done to assess the global variation in size and shape of the skull. The geographic areas and nominal species represented in the analysis comprised the following: 1. Canada (*rixosa*); 2. eastern United States (*allegbeniensis*); 3. central Great Plains (U. S.) (*campestris*); 4. Alaska-Yukon (*eskimo*); 5. eastern Siberia (*pygmaea*); 6. eastern Asia (*pygmaea*); 7. central Asia (*pallida*); 8. western Siberia (*nivalis*); 9. northern Europe (*nivalis*); 10. central Europe (*vulgaris*); 11. western Europe (*vulgaris*); 12. southwestern Asia (*boccamela*); 13. Balkan Peninsula (*boccamela*); 14. Italy and adjacent mediterranean France (*boccamela*); 15. Iberian Peninsula (*iberica*); 16. northwest Africa (*numidica*); 17. Egypt (*subpalmata*).

A smaller number of variables, but a larger number of geographic samples (including REICHSTEIN's data) were used to increase resolution in the area of greatest geographic variation. The geographic areas represented in this analysis were as above, but central Europe is represented by separate samples for: 1. northern Germany; 2. central and western Germany; 3. southern Germany; 4. Silesia; 5. Poland; 6. Switzerland; and 7. Sardinia is separated from Italy.

Both sets of samples were also subjected to distance analysis, using the generalized distance (D), to study the morphometric relationships among geographic populations. To this end, the matrix of generalized distances among geographic forms was analyzed by cluster analysis (UPGMA, SNEATH and SOKAL 1973). Males and females were analyzed separately.

Results

Cranial variation in males

The results of the multiple discriminant function analysis of the subsamples of males are presented in table 1 and figure 1. The graph (Fig. 1) shows the centroid of each group and the dispersion of individuals around them (polygons) plotted onto the first two canonical variates. The relative importance of the different variates in the discrimination of samples is listed in table 1 and shown by the character vector diagram in figure 1. A little over 70 percent of the cranial variation is explained by the first canonical axis, 16.29 percent by the second and 4.11 by the third axis (Table 1). All variates, except ONL contribute to a considerable extent to discrimination on the first axis. This axis discriminates among size classes, from small on the left to large on the right. On the second axis, BSW and GWP4 contribute to discrimination to an important degree (Table 1).

The bivariate plot of the centroids and their respective polygons clearly shows an ordination into two separate nonoverlapping groups, with *M. n. subpalmata* on the one hand and all the other geographic samples on the other. A closer examination reveals that the latter group is composed of two, or three, subsidiary groupings. On the left of the graph we see the largely overlapping polygons representing the small North American, Siberian, eastern Asian and northern European forms and on the right a similar overlapping cluster of the larger forms from temperate Europe, the Mediterranean area and southwestern Asia. These two clusters are linked by the sample from central Europe. A

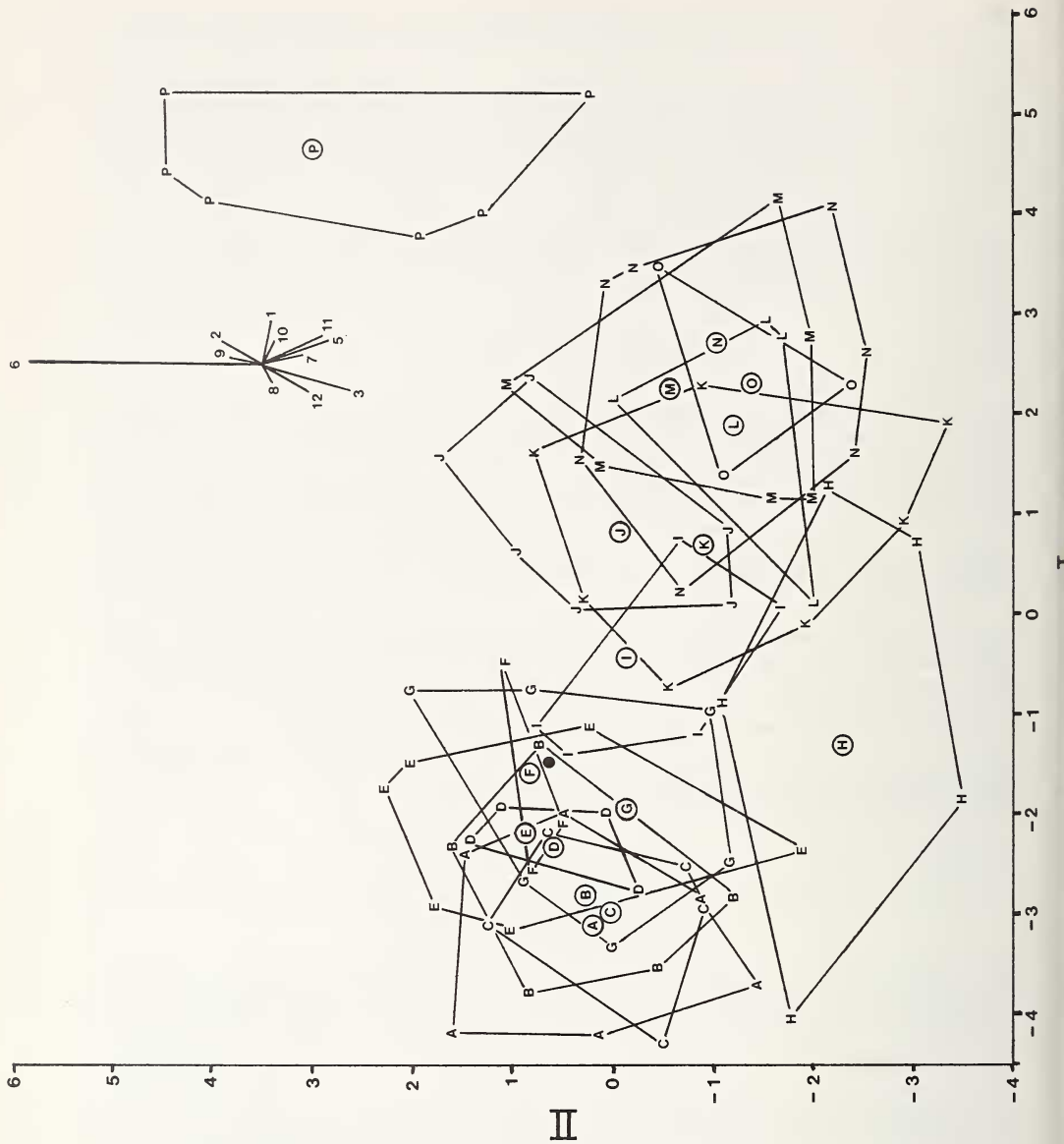


Fig. 1. Graph showing the projection of the centroids and sample dispersions (polygons) of 16 geographic samples of *Mustela nivalis* males onto the first two canonical axes. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegheensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Eastern Asia (*pygmaea*); G: Western Siberia (*nivalis*); H: Central Asia (*pallida*); I: Central Europe (*vulgaris*); J: Iberian Peninsula (*iberica*); K: Western Europe (*vulgaris*); L: Southwestern Asia (*boccamela*); M: Italy and adjacent areas (*boccamela*); N: Balkan Peninsula (*boccamela*); O: Northwestern Africa (*numidica*); P: Egypt (*subpalmata*). The solid dot represents the centroid of two specimens from northern Europe (*nivalis*). The character vector diagram illustrates the relative contribution of the original variates to the canonical variates (numbers as listed in the text)

Table 1. First three standardized canonical vectors from the discriminant function analysis of 12 cranial variables from *Mustela nivalis*

The number in parentheses is the percentage of the variance of each variable contributed to the canonical axis

Variable	Standardized canonical vectors			Cumulative percent
	1	2	3	
1. CBL	0.451 (92.53)	-0.070 (0.13)	-0.024 (0.00)	92.66
2. IOW	0.203 (69.73)	0.388 (15.35)	0.602 (2.09)	87.17
3. WPOP	-0.232 (50.16)	-0.881 (43.40)	0.250 (0.20)	93.76
4. ONL	-0.014 (1.22)	-0.048 (0.90)	-0.810 (14.27)	16.39
5. WPC	0.267 (64.66)	-0.635 (22.13)	0.027 (0.00)	86.79
6. BSW	0.026 (0.20)	2.331 (95.28)	-0.748 (0.55)	96.03
7. MW	0.119 (41.55)	-0.395 (27.50)	0.994 (9.84)	78.89
8. LP4	-0.171 (81.84)	-0.088 (1.30)	0.687 (4.48)	87.62
9. GWP4	0.071 (40.69)	0.304 (45.10)	0.005 (0.00)	85.79
10. LM1	0.263 (96.16)	-0.120 (1.21)	-0.267 (0.34)	97.71
11. GDM1	0.310 (69.10)	-0.605 (15.83)	0.894 (1.95)	86.88
12. Lpm	-0.254 (71.83)	-0.458 (14.04)	-1.712 (11.05)	96.92
Percent trace	70.70	16.29	4.11	
Cumulative percent	70.70	86.99	91.09	

Test of equality of group centroids: $F = 7.35$ with 96 and 1081 degrees of freedom. $P < 0.001$.

Table 2. First two standardized canonical vectors from the discriminant function analysis of four cranial variables from *Mustela nivalis* males

Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Standardized canonical vectors		Cumulative percent
	1	2	
1. CBL	-0.698 (98.13)	-1.258 (1.19)	99.32
2. IOW	0.122 (72.86)	-0.484 (4.31)	77.17
3. MW	-0.399 (86.62)	2.544 (13.27)	99.89
4. ZW	-0.036 (11.04)	-0.919 (26.85)	37.89
Percent trace	87.78	6.95	
Cumulative percent	87.78	94.73	

Test of equality of group centroids: $F = 11.46$ with 88 and 1905 degrees of freedom. $P < 0.0001$.

third subsidiary group is represented by the small sample from Central Asia situated below, and marginally overlapping the two previous groups. The character vectors (Fig. 1 and Table 1) indicate that the boreal and temperate weasels differ from one another principally in size, lying along a common size axis, which slopes gently from left to right. The sample from central Asia is somewhat intermediate in size relative to the last to groups, but differs from them to some extent in the shape of the skull (relatively greater WPOP, WPC and Lpm). The Egyptian weasel (*subpalmata*), on the other hand, differs from all the others in size, as well as in shape (relatively broader BSW, GWP4 and IOW).

The results of a UPGMA cluster analysis of the matrix of Generalized Distances among the geographic populations are shown in the form of a phenogram (Fig. 2). All small northern forms make up one cluster, which is joined by the central Asian form at a lower

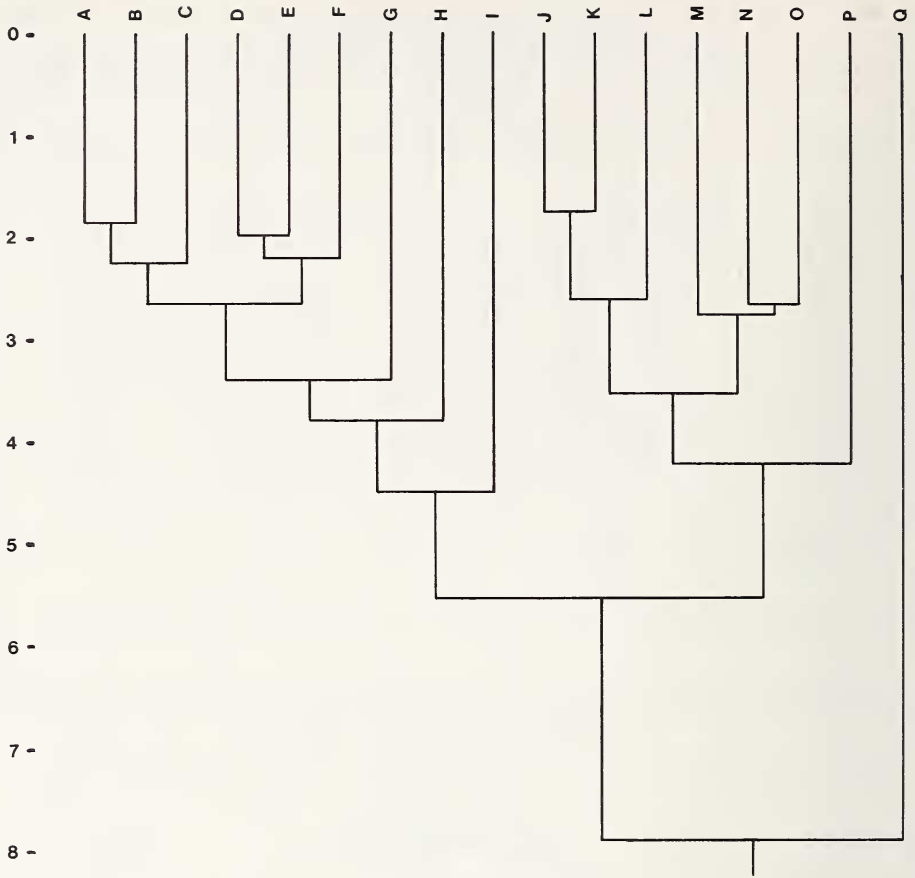


Fig. 2. Distance phenogram summarizing the morphometric relationships among 17 geographic samples of male *Mustela nivalis*. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Western Siberia (*nivalis*); D: Eastern Siberia (*pygmaea*); E: Eastern Asia (*pygmaea*); F: Northern Europe (*nivalis*); G: Eastern U.S. (*allegbeniensis*); H: Central Great Plains, U.S. (*campestris*); I: Central Asia (*pallida*); J: Balkan Peninsula (*boccamela*); K: Italy (*boccamela*); L: Southwestern Asia (*boccamela*); M: Central Europa (*vulgaris*); N: Iberian Peninsula (*iberica*); O: Western Europe (*vulgaris*); P: Northwestern Africa (*numidica*); Q: Egypt (*subpalmata*)

level (4.47), and all large temperate and southern forms constitute a similarly structured cluster. The Egyptian weasel is most remote and joins the others at $D = 7.91$.

It is clear from examining the above results, that the greatest cranial variation is found in the western Palearctic. Results of the discriminant function analysis of a larger number of geographic samples, but a smaller number of variates (CBL, IOW, MW, and ZW, including REICHSTEIN's [1957] data) provided increased resolution of the general pattern of variation in this area. The broad pattern of geographic variation that emerged from the analysis is depicted in two ways. Firstly, the results are shown as a graph of the centroids and their 95% confidence circles on the first two canonical axes (Fig. 3). Secondly, to place the variation in a geographical context, the results are projected on a map of the distributional range as graphic indices of each population's morphometric state and as generalized distances between neighboring populations (Fig. 4).

The plot of the centroids shows the weasel populations arranged from small, on the

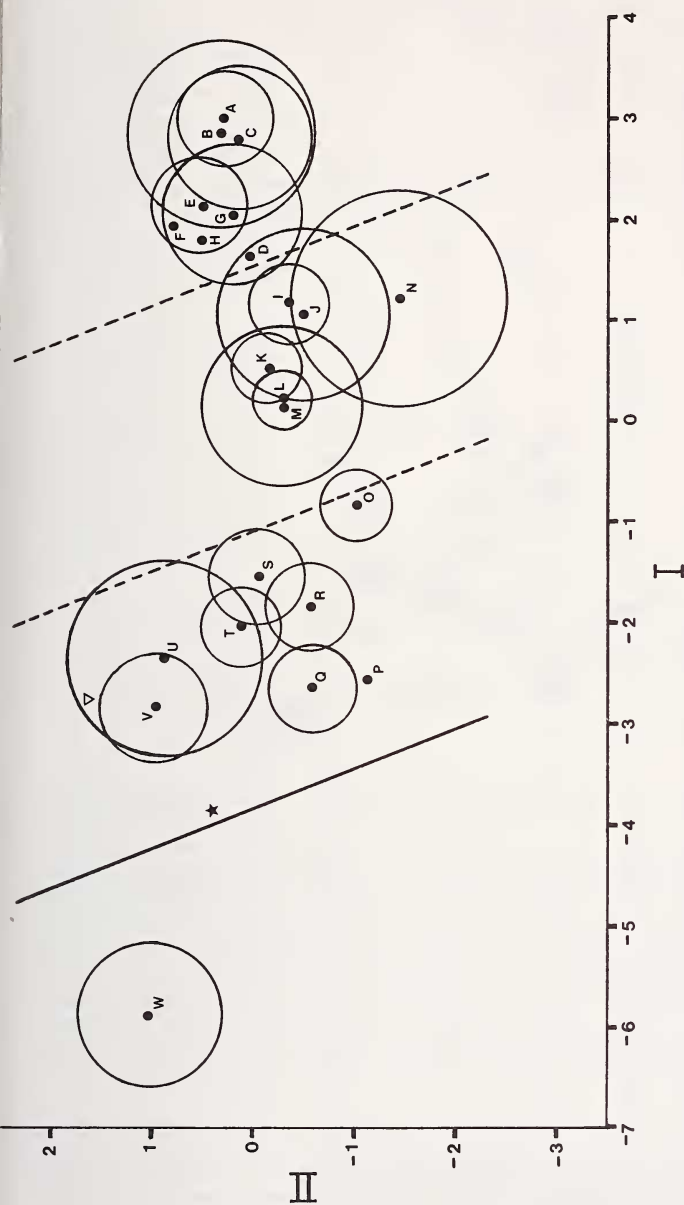


Fig. 3. Canonical graph (axes 1 and 2) of the centroids and their respective 95% confidence circles of 23 geographic samples of male *Mustela nivalis* based on four cranial variables. The broken diagonal lines separate overlapping forms of *M. nivalis* ranging from small on the right to intermediate and large on the left. The solid diagonal line marks the separation of *subpalmata*, which does not overlap with the other forms. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegbeniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Eastern Asia (*pygmaea*); G: Western Siberia (*nivalis*); H: Northern Europe (*nivalis*); I: Switzerland (*vulgaris*); J: Southern Germany (*vulgaris*); K: Western and central Germany (*vulgaris*); L: Northern Germany (*vulgaris*); M: Poland (*vulgaris*); N: Central Asia (*pallida*); O: Western Europe (*vulgaris*); P: Northwestern Africa (*numidica*); Q: Balkan and Danube states (*boccamela*); R: Silesia (*vulgaris*); S: Iberian Peninsula (*iberica*); T: Italy (*boccamela*); U: Southwestern Asia (*boccamela*); V: Sardinia (*boccamela*); W: Egypt (*subpalmata*). Two single specimens from the Azores and Crete (*galianthas*), inverted triangle and star respectively, were scored a posteriori and plotted to show their morphometric relationships.

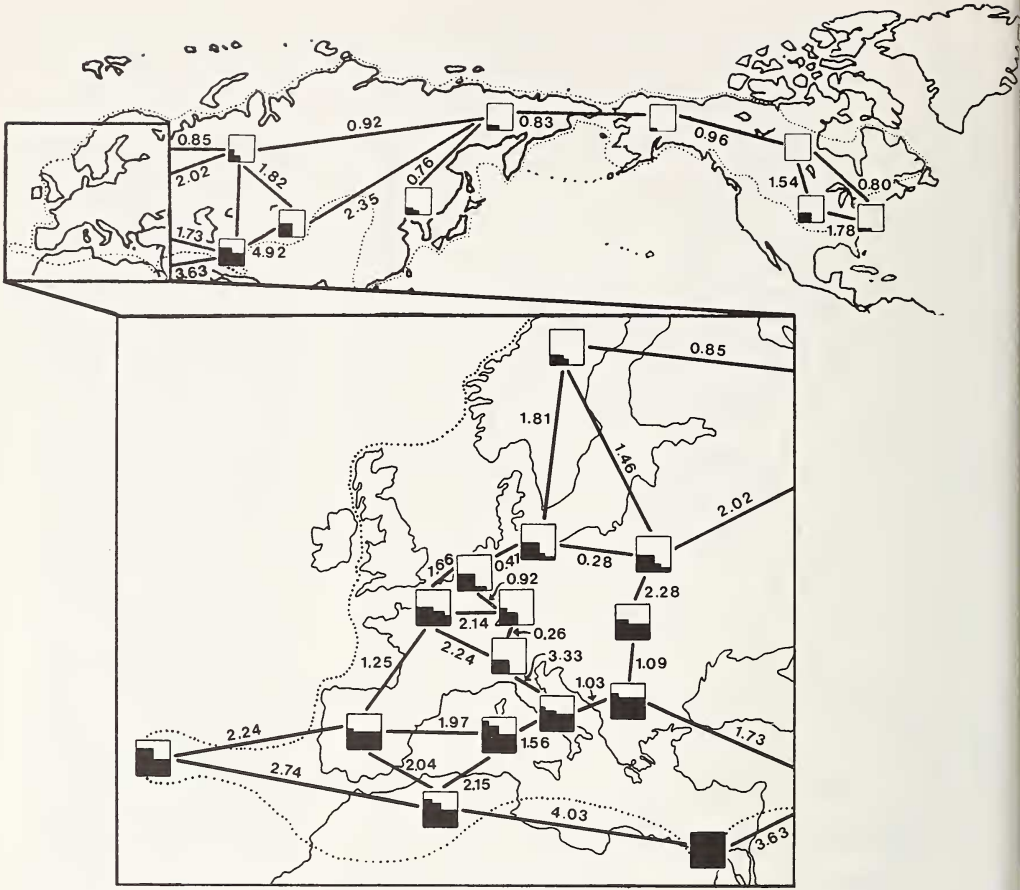


Fig. 4. Geographic variation in the skulls of male *Mustela nivalis*. The squares indicate the morphometric position of the regional forms on the first canonical axis from smallest (no black) to largest (all black). The numbers and lines joining the squares give the generalized distance (D) and a comparative measure of the spatial separation of neighboring populations represented by the samples. In North America and Asia from east to west: Eastern U.S. (*allegbeniensis*); Central Great Plains, U.S. (*campestris*); Canada (*vixosa*); Alaska-Yukon (*eskimo*); Eastern Siberia (*pygmaea*); Eastern Asia (*pygmaea*); Central Asia (*pallida*); West Siberia (*nivalis*) (north); Southwestern Asia (*boccamela*) (south). In Europe and North Africa from north to south and east to west: Northern Europa (*nivalis*); Poland (*nivalis*); Northern Germany (*nivalis*); Central and Western Germany (*vulgaris*); Silesia (*vulgaris*); Southern Germany (*vulgaris*); Western Europe (*vulgaris*); Switzerland (*vulgaris*); Balkan Peninsula (*boccamela*); Italy (*boccamela*); Sardinia (*boccamela*); Iberian Peninsula (*iberica*); Azores; Egypt (*subpalmata*); Northwest Africa (*numidica*)

right, to large forms on the left (see table 2 for standardized canonical vectors). The centroids with their largely overlapping confidence regions form a graded series from small boreal forms to intermediate temperate forms, to large mediterranean forms, whereas the Egyptian weasel is separated from all the others by a distinct gap.

The distribution of morphological forms and D values separating neighbours show clearly that the samples from boreal areas across North America and Eurasia, although separated by large distances in space, differ from each other relatively little morphometrically (Fig. 4). In the western Palaeartic, on the other hand, there is considerable

Table 3. Results of univariate Newmann-Student-Keuls test on four variables of male weasels
Sample designations as in Fig. 3

CBL					IOW				
Sample	N	Subspecies	Mean	Subset	Sample	N	Subspecies	Mean	Subset
A	18	<i>rixosa</i>	31.15		A	18	<i>rixosa</i>	6.34	
C	10	<i>alleggh</i>	31.69		B	7	<i>eskimo</i>	6.61	
B	7	<i>eskimo</i>	31.69		C	10	<i>alleggh</i>	6.78	
E	19	<i>pygmae</i>	32.93		D	4	<i>campes</i>	6.79	
F	3	<i>pygmae</i>	33.09		F	3	<i>pygmae</i>	6.98	
G	11	<i>nivali</i>	33.34		E	19	<i>pygmae</i>	7.01	
H	5	<i>nivali</i>	33.63		H	5	<i>nivali</i>	7.28	
D	4	<i>campes</i>	34.00		G	11	<i>nivali</i>	7.30	
I	27	<i>vulgar</i>	35.13		I	27	<i>vulgar</i>	7.43	
J	8	<i>vulgar</i>	35.46		J	8	<i>vulgar</i>	7.49	
N	6	<i>pallid</i>	35.48		N	6	<i>pallid</i>	7.75	
K	38	<i>vulgar</i>	36.28		K	38	<i>vulgar</i>	7.76	
M	9	<i>vulgar</i>	37.02		L	53	<i>vulgar</i>	7.98	
L	53	<i>vulgar</i>	37.04		M	9	<i>vulgar</i>	8.08	
O	34	<i>vulgar</i>	39.22		O	34	<i>vulgar</i>	8.66	
S	19	<i>iberic</i>	40.20		R	23	<i>vulgar</i>	8.77	
R	23	<i>vulgar</i>	41.00		S	19	<i>iberic</i>	8.89	
T	26	<i>boccam</i>	41.18		T	26	<i>boccam</i>	8.94	
U	7	<i>boccam</i>	41.69		M	24	<i>boccam</i>	9.28	
V	16	<i>boccam</i>	42.66		P	4	<i>numidi</i>	9.29	
Q	24	<i>boccam</i>	42.68		V	16	<i>boccam</i>	9.32	
P	4	<i>numidi</i>	42.86		U	7	<i>boccam</i>	9.36	
W	10	<i>subpal</i>	48.56		W	10	<i>subpal</i>	10.73	
MW					ZW				
A	18	<i>rixosa</i>	14.27		B	7	<i>eskimo</i>	15.54	
B	7	<i>eskimo</i>	14.46		A	18	<i>rixosa</i>	15.75	
C	10	<i>alleggh</i>	14.70		C	10	<i>alleggh</i>	16.33	
E	19	<i>pygmae</i>	15.46		G	11	<i>nivali</i>	16.59	
G	11	<i>nivali</i>	15.48		E	19	<i>pygmae</i>	16.70	
D	4	<i>campes</i>	15.63		D	4	<i>campes</i>	17.24	
F	3	<i>pygmae</i>	15.80		H	5	<i>nivali</i>	17.30	
N	6	<i>pallid</i>	15.83		F	3	<i>pygmae</i>	17.32	
H	5	<i>nivali</i>	15.91		N	6	<i>pallid</i>	17.69	
I	27	<i>vulgar</i>	16.15		I	27	<i>vulgar</i>	17.75	
J	8	<i>vulgar</i>	16.23		J	8	<i>vulgar</i>	17.81	
K	38	<i>vulgar</i>	17.08		K	38	<i>vulgar</i>	18.99	
L	53	<i>vulgar</i>	17.45		L	53	<i>vulgar</i>	19.44	
M	9	<i>vulgar</i>	17.49		M	9	<i>vulgar</i>	19.44	
O	34	<i>vulgar</i>	18.49		O	34	<i>vulgar</i>	21.09	
S	19	<i>iberic</i>	19.66		S	19	<i>iberic</i>	22.08	
R	23	<i>vulgar</i>	19.70		R	23	<i>vulgar</i>	22.47	
T	26	<i>boccam</i>	20.19		T	26	<i>boccam</i>	22.59	
P	4	<i>numidi</i>	20.23		P	4	<i>numidi</i>	22.61	
Q	24	<i>boccam</i>	20.60		U	7	<i>boccam</i>	22.70	
V	7	<i>boccam</i>	20.90		V	16	<i>boccam</i>	22.90	
V	16	<i>boccam</i>	21.29		Q	24	<i>boccam</i>	23.16	
W	10	<i>subpal</i>	24.94		W	10	<i>subpal</i>	27.43	

morphometric change over relatively small distances, generally taking the form of a north-south cline of increasing size. The smallest morphs occur in northern Europe and the largest in the Mediterranean area. The existence of this size cline was demonstrated previously by REICHSTEIN (1957). Exceptions to this general north-south trend are the populations from higher altitudes in Southern Germany and Switzerland. These are markedly smaller, approaching the boreal forms in size.

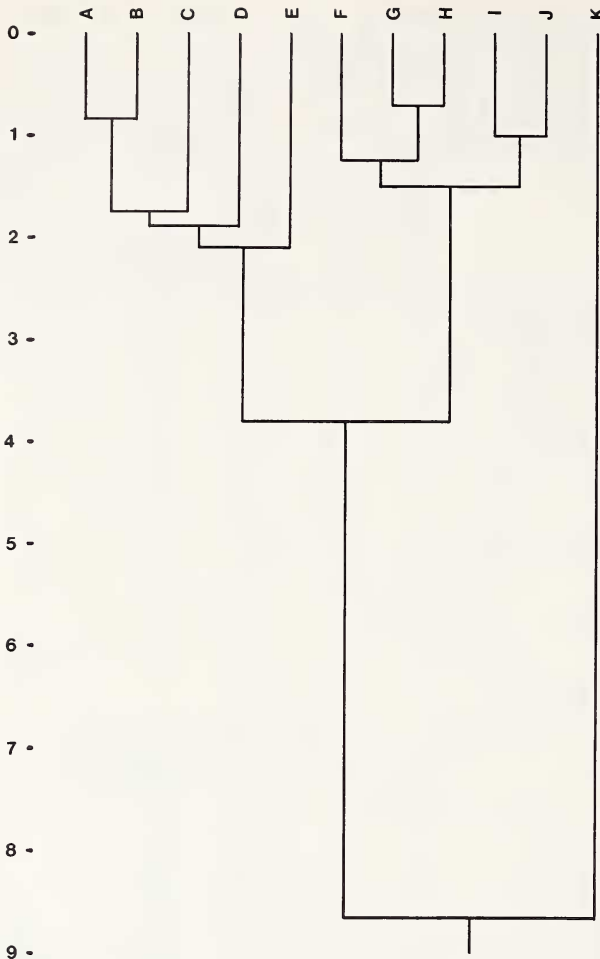


Fig. 5. Distance phenogram summarizing the morphometric relationships of 11 geographic samples of female *Mustela nivalis*. A: Canada (*rixosa*); B: Eastern U.S. (*alleggheniensis*); C: Alaska-Yukon (*eskimo*); D: Eastern Siberia (*pygmaea*); E: Central Great Plains, U.S.: (*campestris*); F: Italy (*boccamela*); G: Iberian Peninsula (*iberica*); H: Southwestern Asia (*boccamela*); I: Central Europe (*vulgaris*); J: Western Europe (*vulgaris*); K: Egypt (*subpalmata*)

to-large size and Egyptian weasels parallels that of the males closely. The main difference between male and female samples is the generally smaller distance (D) between the female centroids and the larger distance separating the Egyptian females from all the rest.

The results of the analysis of geographic variation based on four characters (Figs 6 and 7), likewise, resemble those of the males closely, with little variation in the north from North America to northern Europe and relatively precipitous size change from north to south in Europe. The smaller intercentroid distances among female samples, compared to those among male samples, are again noticeable, as well as the much greater distance of the *subpalmata* centroid from all others. The results of the Student-Newmann-Keuls test of

The results of the a posteriori Student-Newmann-Keuls multiple range test confirm the generally north-south gradual size variation in geographic samples and the gap between *subpalmata* and all the others (Table 3). The only gap, in the largely overlapping nonsignificant subsets, is that between the smaller central European forms (I-L) and the western European-Iberian subset (O-S).

Cranial variation in females

The results of the analyses of female skulls were similar to those obtained for the males. Females were represented in lower numbers in collections and were lacking entirely for some of the geographic subsamples. Because of the reduced geographic representation of females and the similarity of the results for both sexes, it suffices to list the standardized canonical vectors (Table 4) and to show the results of the cluster analysis of the distances among samples of females from different geographic areas (Fig. 5). The clustering of female weasels in three main clusters representing boreal small sized, temperate to mediterranean intermediate-

Table 4. First three standardized canonical vectors from a discriminant function analysis of 12 cranial variables from *Mustela nivalis* females

Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Canonical vectors			Cumulative percent
	1	2	3	
1. CBL	-0.864 (99.99)	-0.010 (0.00)	-0.026 (0.00)	100
2. IOW	0.514 (82.35)	1.398 (16.44)	1.020 (1.19)	99.98
3. WPOP	0.149 (89.11)	0.019 (0.03)	-0.854 (10.85)	99.99
4. ONL	0.386 (91.98)	-0.634 (6.70)	-0.757 (1.30)	99.98
5. WPC	-0.548 (97.44)	0.499 (2.17)	-0.567 (0.38)	99.99
6. BSW	-0.410 (62.85)	-1.883 (35.75)	1.006 (1.39)	99.99
7. MW	-0.201 (93.10)	0.331 (6.84)	-0.084 (0.06)	100
8. LP4	-0.143 (88.79)	0.310 (11.20)	0.000 (0.00)	99.99
9. GWP4	-0.076 (38.01)	0.491 (43.30)	0.872 (18.68)	99.99
10. LM1	0.344 (98.43)	-0.264 (1.56)	-0.022 (0.00)	99.99
11. GDM1	-0.558 (96.39)	0.657 (3.60)	0.023 (0.00)	99.99
12. Lpm	0.723 (97.76)	-0.592 (1.76)	-0.824 (0.46)	99.98
Percent trace	92.28	6.41	1.30	
Cumulative percent	92.28	98.70	100	

Test of equality of group centroids: $F = 7.76$ with 36 and 133 degrees of freedom. $P < 0.001$.

the four variables (Table 5) confirms the continuous nature of the size variation and the smaller differences among female samples, with the obvious exception of the sample of *subpalmata*. The greater difference between *subpalmata* females and females of all the others forms, compared to that in the males, points to the existence of a male-female size relationship in Egyptian weasels that differs from that in the other taxa. This brings us to a consideration of sexual dimorphism of size.

Variation in sexual dimorphism of size

REICHSTEIN (1957) pointed out that the difference in size between the sexes in *M. nivalis* increases with overall size. In the present samples, for instance, the difference in mean condylobasal length of males and females of the small boreal forms is relatively slight, with the length of the female skull averaging 93 % of that of the male skull (range 90–97 %). In the large mediterranean morphs, on the other hand, the difference is much greater. The female skull length in these forms averages only 85 % of the male skull length (range 83–88 %). An apparent exception is the Egyptian weasel. The mean condylobasal length of the female Egyptian weasel sample constituted about 90 % of the mean of the same length in males.

To investigate the relationship of size in females and males further, the logarithm of the mean condylobasal length of females was plotted against that of males of the same geographic population. Inspection of the resulting pattern suggests a linear relationship of size between the sexes in geographic populations of *M. nivalis*, with the exception of the Egyptian sample, which clearly deviates from the common trend (Fig. 8). The equation describing the relationship (Model II regression, SOKAL and ROHLF 1981) shows that size in females increases at a lower rate than that in males, i.e. the relation is allometric. The goodness of fit index ($r^2 = .86$) indicates that the regression describes the relationship effectively. The mean size of the female Egyptian weasel predicted by the regression (38.0 mm) is less than the actually observed value (43.5 mm). Thus the growth rate in females approaches that of the males more closely in this taxon.

Table 5. Results of univariate Student-Newmann-Keuls test on four variables in female weasels
Sample designations as in Fig. 6

Sample	N	CBL			Sample	N	IOW		
		Subspecies	Mean	Subset			Subspecies	Mean	Subset
A	10	<i>rixosa</i>	28.83		A	10	<i>rixosa</i>	5.78	
B	5	<i>eskimo</i>	29.55		C	4	<i>alleghe</i>	6.02	
E	5	<i>pygmae</i>	29.59		E	5	<i>pygmae</i>	6.04	
C	4	<i>alleghe</i>	30.09		B	5	<i>eskimo</i>	6.16	
H	16	<i>vulgar</i>	30.82		D	2	<i>campes</i>	6.23	
D	2	<i>campes</i>	30.96		H	16	<i>vulgar</i>	6.27	
K	15	<i>vulgar</i>	31.14		K	15	<i>vulgar</i>	6.35	
G	5	<i>vulgar</i>	31.26		J	17	<i>vulgar</i>	6.48	
J	17	<i>vulgar</i>	31.67		G	5	<i>vulgar</i>	6.50	
F	9	<i>nivali</i>	31.89		F	9	<i>nivali</i>	6.62	
I	6	<i>boccam</i>	32.53		I	6	<i>boccam</i>	6.65	
M	2	<i>boccam</i>	33.66		N	7	<i>vulgar</i>	6.94	
N	7	<i>vulgar</i>	34.09		L	9	<i>vulgar</i>	7.12	
L	9	<i>vulgar</i>	34.29		M	2	<i>boccam</i>	7.12	
O	4	<i>boccam</i>	35.08		O	4	<i>boccam</i>	7.17	
P	11	<i>iberic</i>	35.25		P	11	<i>iberic</i>	7.34	
Q	8	<i>subpal</i>	43.56		Q	8	<i>subpal</i>	8.91	
				MW					ZW
B	5	<i>eskimo</i>	12.91		B	5	<i>eskimo</i>	13.84	
A	10	<i>rixosa</i>	13.33		E	5	<i>pygmae</i>	14.16	
E	5	<i>pygmae</i>	13.47		A	10	<i>rixosa</i>	14.18	
H	16	<i>vulgar</i>	13.69		H	16	<i>vulgar</i>	14.82	
C	4	<i>alleghe</i>	13.76		C	4	<i>alleghe</i>	14.90	
F	9	<i>nivali</i>	13.97		G	5	<i>vulgar</i>	15.28	
G	5	<i>vulgar</i>	14.02		D	2	<i>campes</i>	15.48	
D	2	<i>campes</i>	14.03		K	15	<i>vulgar</i>	15.51	
K	15	<i>vulgar</i>	14.13		F	9	<i>nivali</i>	15.53	
J	17	<i>vulgar</i>	14.55		I	6	<i>boccam</i>	15.85	
I	6	<i>boccam</i>	14.90		J	17	<i>vulgar</i>	15.94	
L	9	<i>vulgar</i>	15.39		M	2	<i>boccam</i>	17.16	
N	7	<i>vulgar</i>	15.69		L	9	<i>vulgar</i>	17.17	
M	2	<i>boccam</i>	15.90		N	7	<i>vulgar</i>	17.30	
O	4	<i>boccam</i>	16.31		O	4	<i>boccam</i>	17.54	
P	11	<i>iberic</i>	16.40		P	11	<i>iberic</i>	18.03	
Q	8	<i>subpal</i>	21.62		Q	8	<i>subpal</i>	23.47	

Table 6. First two standardized canonical vectors from the discriminant function analysis of four cranial variables from *Mustela nivalis* females

Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Standardized canonical vectors		Cumulative percent
	1	2	
1. CBL	0.411 (88.38)	1.092 (9.34)	97.72
2. IOW	-0.445 (93.61)	0.898 (5.72)	99.33
3. MW	0.441 (87.24)	-1.175 (9.27)	96.51
4. ZW	0.559 (93.52)	-0.486 (1.06)	94.58
Percent trace	92.27	5.47	
Cumulative percent		97.74	

Test of equality of group centroids: $F = 6.190$ with 64 and 452 degrees of freedom. $P < 0.0001$.

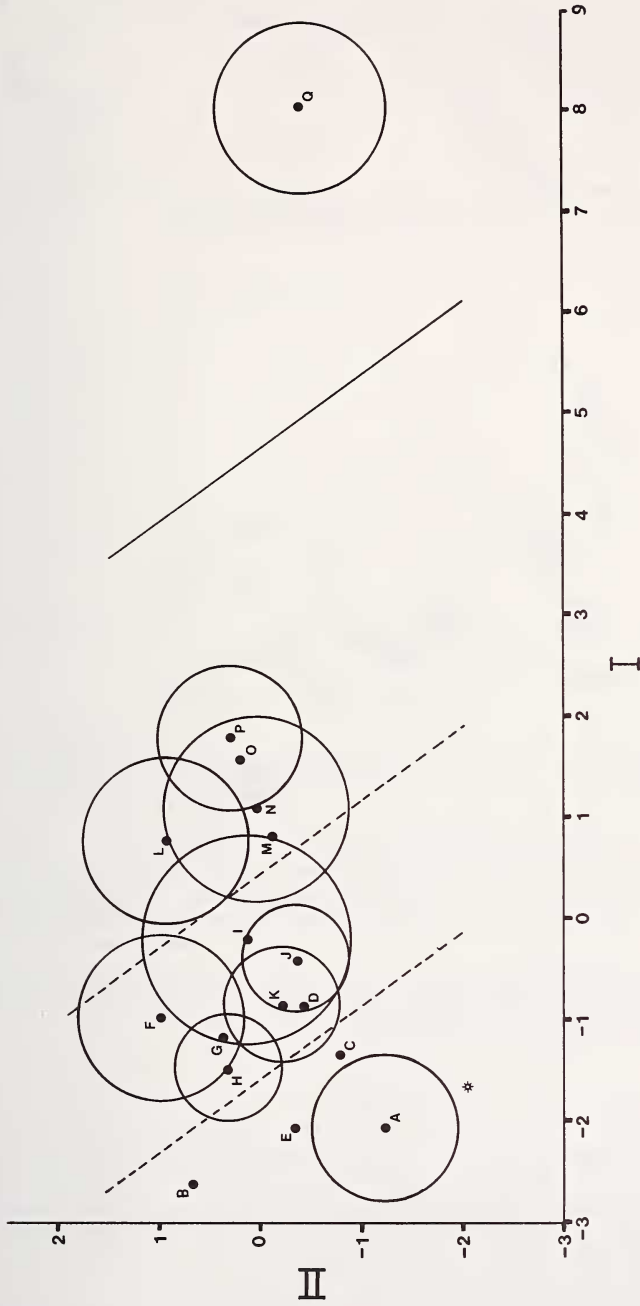


Fig. 6. Canonical graph showing the centroids and respective 95% confidence circles of 17 geographic samples of female *Mustela nivalis*. No confidence circles for samples of less than six specimens were calculated. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegbeniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Northern Europe (*nivalis*); G: Southern Germany (*vulgaris*); H: Switzerland (*vulgaris*); I: Balkan Peninsula (*boccamela*); J: Northern Germany (*vulgaris*); K: Central and Western Germany (*vulgaris*); L: Western Europe (*vulgaris*); M: Southwestern Asia (*boccamela*); N: Silesia (*vulgaris*); O: Italy (*boccamela*); P: Iberian Peninsula (*iberica*); Q: Egypt (*subpalmata*). The asterisk represents a single specimen of *M. n. russelliana* from Szechwan, scored a posteriori

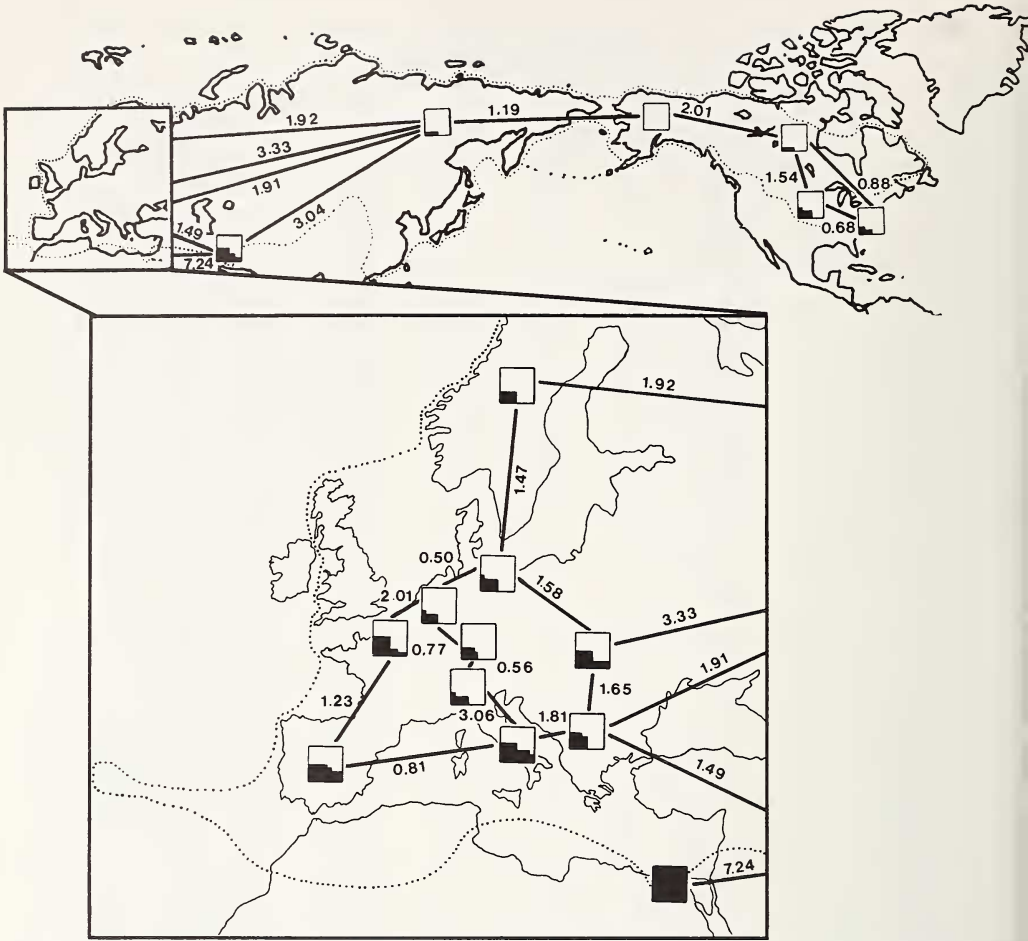


Fig. 7. Geographic variation in the skulls of female *Mustela nivalis*. In North America and Asia from east to west: Eastern U.S. (*allegheniensis*); Central great plains (*campestris*); Canada (*rixosa*); Alaska-Yukon (*eskimo*); Eastern Siberia (*pygmaea*); Southwestern Asia (*boccamela*). In Europe and North Africa, from north to south and east to west: Northern Europe (*nivalis*); Northern Germany (*vulgaris*); Central and Western Germany (*vulgaris*); Silesia (*vulgaris*); Southern Germany (*vulgaris*); Western Europe (*vulgaris*); Switzerland (*vulgaris*); Balkan Peninsula (*boccamela*); Italy (*boccamela*); Iberian Peninsula (*iberica*); Egypt (*subpalmata*). Further details as in Fig. 4

Discussion

The results of the craniometric analyses presented above support the view that all Holarctic weasels of the taxa included in this study are members of one variable species, with the notable exception of *subpalmata*. The latter taxon differs both morphometrically and with respect to sexual dimorphism of size from all the other taxa. These differences suggest the possible existence of underlying genetic and/or epigenetic mechanisms in *subpalmata* that differ from those in the other taxa. There is thus sufficient evidence to suspect that *subpalmata* may have evolved independently for a considerable period of time and may be specifically distinct from *M. nivalis*. This requires confirmation from the study of other character sets, including molecular data.

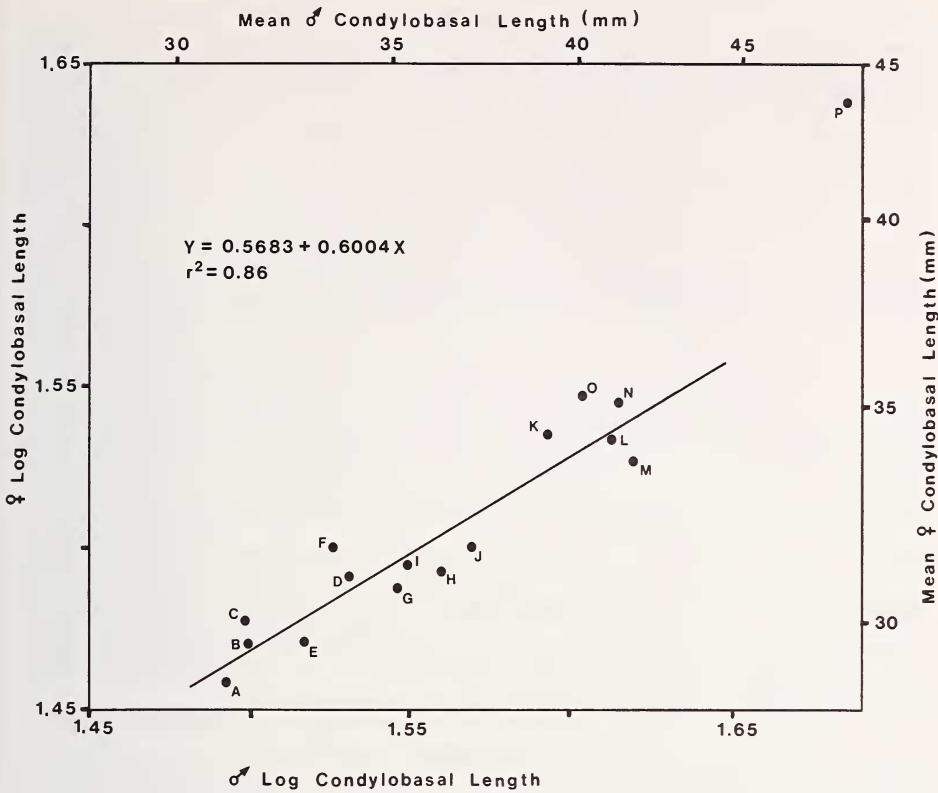


Fig. 8. Sexual dimorphism of size in *Mustela nivalis*. The equation describes the linear relationship between size of males and of females in populations of *M. nivalis* (without *subpalmata*) varying in size from small to large; r^2 is a measure of goodness of fit. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*alleggheniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Northern Europe (*nivalis*); G: Switzerland (*vulgaris*); H: Central and Western Germany (*vulgaris*); I: Southern Germany (*vulgaris*); J: Northern Germany (*vulgaris*); K: Western Europa (*vulgaris*); L: Silesia (*vulgaris*); M: Southwestern Asia (*boccamela*); N: Italy (*boccamela*); O: Iberian Peninsula (*iberica*); P: Egypt (*subpalmata*)

All other taxa in this study represent overlapping gradations in morphology and share a common sexual size dimorphism. Both, morphology of the skull and the difference in size between the sexes, are predominantly effectuated by overall size. The conclusion is that these taxa constitute one species, *M. nivalis*. The results of the morphometric analysis do not agree with the great number of subspecies recognized in the literature and suggest that a reduced number would be more realistic. A complete taxonomic revision, using all available characters and maximum geographic representation, is indicated. Such a revision clearly lies outside the scope of the present study. However, the results of this analysis support a breakdown of the populations studied into three subspecific groups: 1. The *nivalis* group. A group of small weasels, characterized by white winter pelage and distributed throughout the northern coniferous biome of Eurasia and North America. 2. The *vulgaris* group (including *boccamela* and *numidica*). A group of intermediate to large sized weasels, characterized by brown winter pelage and distributed in the temperate deciduous biome and Mediterranean region of the western Palearctic region. 3. A Central Asian group of intermediate sized weasels (*pallida*), with white winter pelage (HEPTNER et al. 1974).

This represents a reduction in the number of taxa distinguished by FRANK (1985) in the western Palearctic. As FRANK (1985) pointed out, and the results of this study confirm, *vulgaris* and *boccamela* are difficult to delineate. Populations designated to these subspecies form a gradual north-south cline, lacking the marked morphological discontinuity that characterizes the transition between *nivalis* and *vulgaris*. They are, therefore, best combined into one taxonomic category. The existence of a *numidica* group, postulated by FRANK (1985) as being an independent species (type locality: Tangiers, Morocco) most closely resembling the ancestor of least weasels, is not supported by the morphometric evidence. The northwest African sample is morphometrically not distinct from other Mediterranean weasels (it is closest to samples from the Balkan [$D = 0.92$] and Italy [$D = 1.81$]). It seems, therefore, likely that *M. nivalis* invaded North Africa via Spain during the late Pleistocene, like other Palearctic elements. The weasel from Crete (*galianthas*), one of the insular forms included in the presumed ancestral *numidica* group by FRANK (1985), is represented by one specimen. It was scored and plotted a posteriori (Fig. 3) to gain some idea about its possible affinities. Its position indicates that it is similar to other forms from the Mediterranean area and closest to the topotypic sample of *boccamela* from Sardinia. The time of isolation of the northwest African and island populations in the Mediterranean from those on the European mainland may be comparable to that of the eastern Siberian and North American populations. The respective morphometric differences are approximately of the same magnitude, a consideration that lends some support to this assumption.

The small Central Asian sample is from one locality (Dzharkent = Panfilov) in east Kazakhstan. More samples from central Asia will have to be studied before a clear picture of geographic variation in the area can emerge. A single specimen from Szechwan is similar to the boreal Asian and North American forms (Fig. 6), which suggests that the species entered China from the north.

The great variation of the species in the western Palearctic and the fossil record (KURTÉN 1968) suggest that *M. nivalis* evolved here. It appears highly likely that the small northern forms (*nivalis*) evolved most recently, under the prevailing boreal conditions of the Pleistocene glaciations. Their adaptations to boreal conditions having been perfected, they subsequently spread east throughout northern Asia, invading North America only during the late Pleistocene.

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Zusammenfassung

Morphometrische Analyse der Schädelvariation beim holarktischen Mauswiesel (Mustela nivalis)

Die Schädelvariabilität der Mauswiesel (*Mustela nivalis*) aus verschiedenen Teilgebieten des holarktischen Artareals wurde morphometrisch untersucht. Schädelmaße erwachsener Tiere wurden multivariaten Diskriminanzanalysen unterzogen, um eine Klärung in der Systematik der Mauswiesel herbeizuführen. Die Ergebnisse dieser Analysen zeigen, daß die Populationen verschiedener Teilgebiete, außer die ägyptische (*subpalmata*), einem morphologischen Kontinuum angehören und hauptsächlich in der Größe variieren. Diese Beobachtung stützt die Behauptung, daß diese Populationen einer Art zuzuordnen sind. Die morphometrischen Daten ermöglichen eine Teilung in drei phänotypisch ähnliche subspezifische Gruppen: die *nivalis*-Gruppe, kleine Wiesel der borealen Gebiete der Holarktis; die *vulgaris*-Gruppe, mittel- bis großwüchsige Wiesel, welche die gemäßigten und mediterranen Gebiete der westlichen Palaearktis bewohnen, und eine zentralasiatische Gruppe (*pallida*). Das ägyptische Wiesel ist wahrscheinlich eine selbständige Art.

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